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Diversification and Relationships of Extant Homosporous Lycopods

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ABSTRACT.—A series of phylogenetic analyses using nucleotide sequence data have resolved many aspects of the relationships in a group of land plants that until recently had received comparatively little attention, the homosporous lycopsids (Lycopodiaceae). The family includes no more than 400–500 living species but the group has evolved as an isolated lineage since the Early Devonian (390 Mya). Despite this ancient history, patterns emerging through the phylogenetic analyses imply that most diversification in this group is comparatively recent. The Lower Jurassic stem section *Lycoxylon indicum* indicates a minimum age for the split between *Lycopodium* and *Lycopodiella* at 208 Mya, and reticulate fossil spores from the Early Jurassic indicate that early cladogenesis in *Lycopodium* is of equivalent age. In the diverse predominantly epiphytic *Huperzia* group, biogeographic data indicates that 85–90 % of all living species result from cladogenic events postdating the final rifting of S. America and Africa in Mid to Late Cretaceous. The timing of these events coincides with the radiation of Angiosperms, and the diversification of epiphytic *Huperzia* was likely mediated by the development of broad leaved Angiosperm rain forests. Results indicate a single origin of epiphytism in *Huperzia,* but there have been at least two reversals to the terrestrial habit in the neotropics. The diversification of a large secondarily terrestrial clade, including about 80 montane high altitude species, was likely triggered by the Andean orogeny in the Mid Miocene, no more than 15 Mya.

Lycopsids are an ancient group with an extensive fossil record, and small herbaceous species are among the most easily recognizable and conspicuous elements of the early land flora. Because of their lengthy fossil record, the group was soon recognized as the product of an early cladogenic event in land plant evolution (Banks, 1968, 1975; Bower, 1908). Recent phylogenetic analyses support this view and indicate that lycopsids are sister to all remaining vascular plants (Doyle, 1998; Duff and Nickrent, 1999; Kenrick and Crane, 1997; Kranz and Huss, 1996; Raubeson and Jansen, 1992). The fossil record provides strong evidence that the three extant lineages (Lycopodiaceae, Selaginellaceae and Isoetaceae) also originated in the Palaeozoic. The occurrence of Protolepidodendrales in the Early Devonian (Kenrick and Crane, 1997) suggests a minimum age of 390 Myr for the split between Lycopodiaceae and the ligulate clade including Selaginellaceae and Isoetaceae. Furthermore, the occurrence of Isoetales in the Late Devonian (Kenrick and Crane, 1997) suggests a minimum age of 377 Myr for the split between extant Isoetaceae and Selaginellaceae. Despite the antiquity of these events, little is known about the diversification of the crown groups. Although the fossil record includes taxa showing similarities to extant Lycopodiaceae (Skog and Hill, 1992; Thomas, 1992), Selaginellaceae (Thomas, 1992, 1997) and Isoetaceae (Pigg, 1992; Retallack, 1997), their specific relationships to living species remain unclear.

One of the major problems has been the lack of well developed phylogenetic

hypotheses. Without such hypotheses, there is no way of telling whether the fossils are nested within the crown groups, or are part of the stem lineages. *Isoetes bestonii* Retallack for example has been identified as far back as the Triassic (Retallack, 1997). If shown to be part of the crown group of living *Isoetes,* this would certainly contribute to our understanding of the patterns of diversification of living species.

Separated from the ligulate lycopsids since the Early Devonian, the homosporous lycopods (Lycopodiaceae) have evolved as an independent lineage for at least 390 Myr. Morphologically, living species show striking similarities to some of the oldest vascular plants (Heuber, 1992; Kenrick and Crane, 1997), but from a palaeobotanical perspective Lycopodiaceae have been particularly problematic (Skog and Hill, 1992; Thomas, 1992). The macrofossil record is relatively meager and palaeobotanical work is hampered by recognition problems. Absence of clear morphological synapomorphies for the family makes assignments of fossil taxa difficult, and this is often based on absence of the characteristics of more distinctive groups such as Selaginellaceae. Another problem involves the superficial similarities between Lycopodiaceae and organ systems of other plant groups. These problems notwithstanding, Skog and Hill (1992) hypothesized that the major living groups within Lycopodiaceae were established during the Late Jurassic-Cretaceous. In other words, despite its apparent relict status, modern species diversity in Lycopodiaceae evolved comparatively recently and in parallel with that in more diverse, ecologically prominent groups such as flowering plants.

Over the last couple of years, I and my coauthors have been developing a phylogenetic hypothesis for living species of Lycopodiaceae (Wikström and Kenrick, 1997, 2000a, 2000b; Wikström *et al.*, 1999). Using molecular sequence data from the plastid *rbc*L gene, and from the *trn*L-*trn*F intron and spacer regions, we have conducted a number of phylogenetic analyses at different levels of the hierarchy in the family. These analyses provide empirical support for the idea that most cladogenesis in this ancient family is comparatively recent. Here I review some of the progress that has been made in our understanding of Lycopodiaceae relationships and the implications for interpreting the evolution of the family.

Relationships

Lycopodiaceae monophyly and *Phyllloglossum.*—Recent cladistic analyses have shown that monophyly of Lycopodiaceae is at best weakly supported by morphological characters (Crane, 1990; Kenrick and Crane, 1997). Other studies have failed to identify unequivocal family synapomorphies (Wagner and Beitel, 1992), or indicate that Lycopodiaceae may be paraphyletic to a heterosporous lycopsid clade comprising Selaginellaceae, Isoetaceae and extinct relatives (Bateman, 1992). Molecular characters, on the other hand, furnish very strong support for monophyly of the family (Wikström and Kenrick, 1997, 2000a). Their *rbc*L sequence data unequivocally support Lycopodiaceae monophyly. Furthermore, molecular data resolve a basal split in Lycopodiaceae sep-

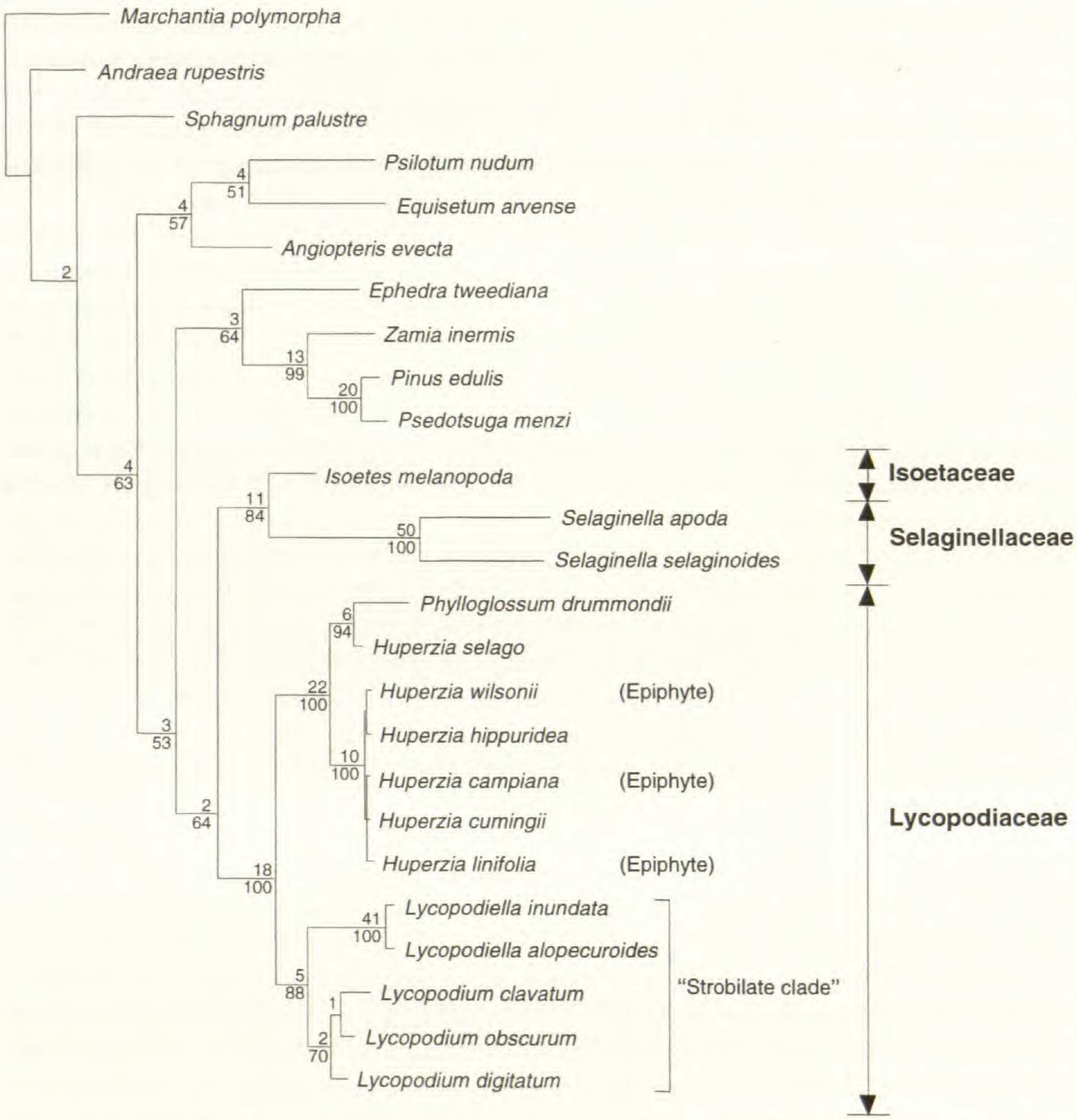

FIG. 1. A single most parsimonious tree indicating relationships of Lycopodiaceae. The tree is reproduced from the analyses of Wikström & Kenrick (1997) of *rbc*L sequence data. The tree is printed as a phylogram with branch lengths proportional to the amount of change along each branch and branch support is indicated by decay indices (above) and bootstrap values (below) for each branch.

arating a "strobilate clade", including *Lycopodium* L. and *Lycopodiella* Holub, from a *Huperzia* Bernh.—*Phylloglossum* Kunze clade. The single most parsimonious tree from Wikström and Kenrick (1997) is reproduced in figure 1 and shows branch support as measured by decay indices (Bremer, 1988; Donoghue *et al.*, 1992) and bootstrap values (Felsenstein, 1985). The support for monophyly of Lycopodiaceae is not entirely unexpected. Perhaps more surprising is the close relationship between *Phylloglossum* and *Huperzia* (Fig. 1). *Phylloglossum* is a monotypic genus occurring only in Australia and New Zealand,

and its highly divergent morphology has made its relationships to other species in Lycopodiaceae difficult to understand. Previous taxonomic treatments have either implicitly or explicitly classified it *incertae sedis* with respect to other groups in the family (Holub, 1985; Øllgaard, 1987; Wagner and Beitel, 1992). A close relationship between *Phylloglossum* and *Huperzia* is however consistent with a number of morphological features such as spore morphology (Breckon and Falk, 1974; Tryon and Lugardon, 1991), sporangial epidermis morphology (Øllgaard, 1975), phytochemistry (Markham *et al.*, 1983) and chromosome number (Blackwood, 1953). Other characters, and in particular the morphology of the perenniating tuber in *Phylloglossum,* led workers such as Bower (1935), Bruce (1976a) and Hackney (1950) to consider a close relationship between *Phylloglossum* and *Lycopodiella.* The *rbc*L sequence data, however, lend unequivocal support for the *Huperzia-Phylloglossum* relationship.

The evolution of *Phylloglossum* from either a *Huperzia* or a *Lycopodium-Lycopodiella* like ancestor implies a remarkable architectural transformation. This include the development of a new organ (perenniating tuber), a substantial reduction of the microphyll-bearing stem system, and the development of a unique stem anatomy. It is noteworthy though that the aspects of morphology likely to be the least affected by this overall architectural change, such as spore and sporangial epidermis morphology and phytochemistry, are also the most consistent with the *rbc*L data in supporting a *Huperzia* relationship.

THE "STROBILATE CLADE".—The "strobilate clade" includes the two genera *Lycopodium* and *Lycopodiella* (sensu Øllgaard, 1987), and although comprising no more than about 40 species each, 11 genera (Holub 1964, 1975, 1983, 1985, 1991) or 13 sections (Øllgaard 1987) have been recognized. My usage of generic and subgeneric names follows that of Øllgaard (1987). One factor contributing to the inflation of subgeneric groups is the segregation of several divergent species as monotypic groups. However, this segregation also reflects a genuine morphological pattern where subgeneric groups are very distinct, each including very similar species, but where there has been considerably more difficult to find similarities between such groups. Works looking at various morphological features such as stem anatomy (Bierhorst, 1971; Jones, 1905; Ogura, 1972), spore morphology (Tryon and Lugardon, 1991; Wilce, 1972), distribution of mucilage canals in trophophylls and sporophylls (Bruce, 1976b), branching pattern (Øllgaard, 1979), chromosome numbers (Wagner, 1992), sporangium epidermis morphology (Øllgaard, 1975), and gametophyte morphology (Bruce, 1976c) have tended to reinforce this pattern, and Øllgaard (1990) hypothesized that the subgeneric groups represent ancient evolutionary lineages.

Despite the success of recent taxonomic work in recognizing subgeneric groups and our increased knowledge about the morphological variation in these plants, there have been few explicit attempts to investigate the phylogenetic relationships of *Lycopodium* and *Lycopodiella.* Wagner and Beitel (1992) analyzed the relationships of N. American species and Wikström and Kenrick (1997) included representatives of both genera in their analyses. Both

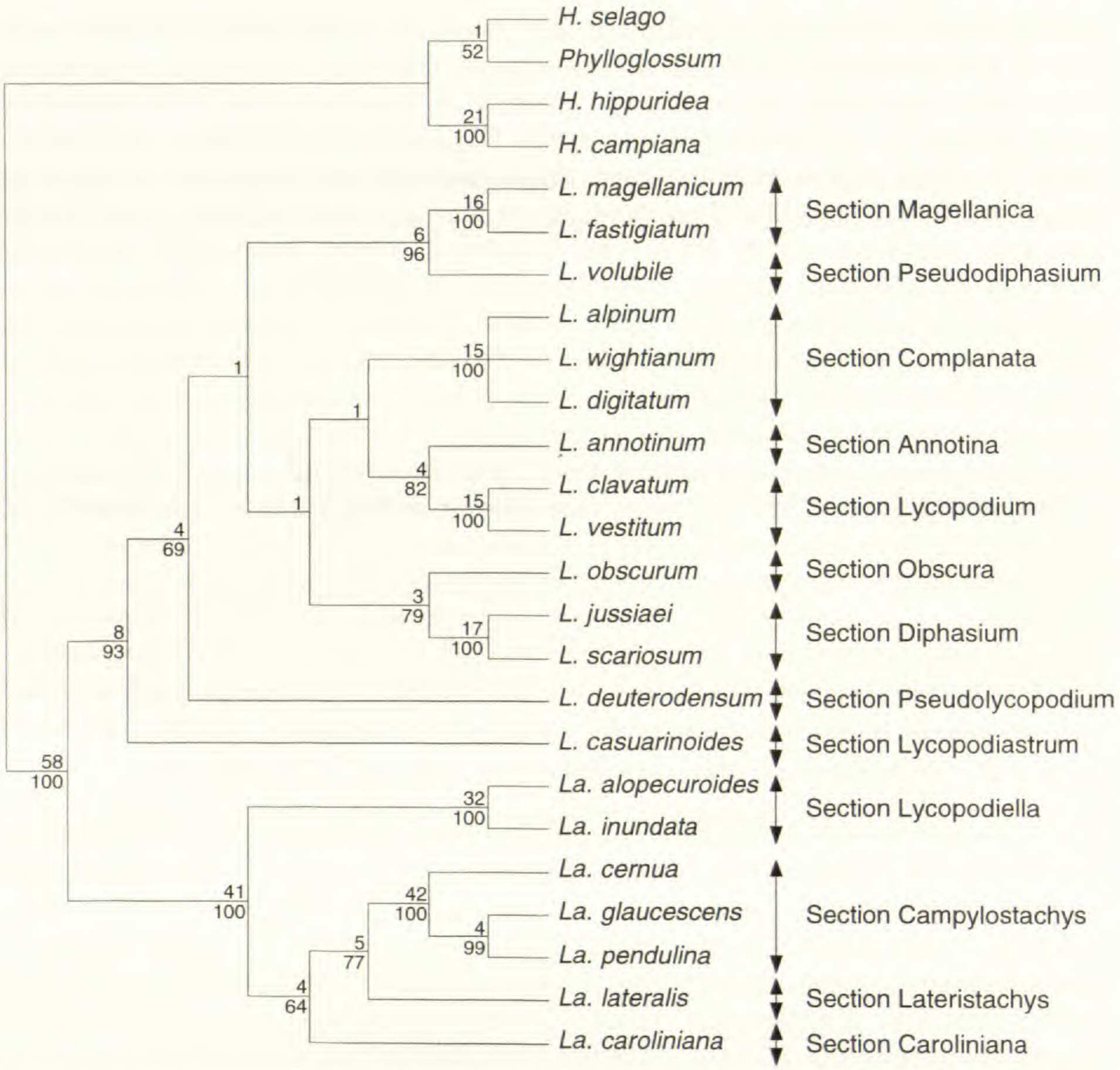

FIG. 2. Strict consensus of two most parsimonious trees indicating relationships within the "strobilate clade". The tree is reproduced from the analyses of Wikström and Kenrick (2000b) of combined *rbc*L gene and *trn*L intron sequence data. Branch support is indicated by decay indices (above) and bootstrap values (below) for each branch. Subgeneric groups (sections sensu Øllgaard, 1987) are shown to the right.

studies however, only included a limited number of species and the majority of the subgeneric groups recognized were not included. To address the relationships of *Lycopodium* and *Lycopodiella,* and specifically the relationships among subgeneric groups, we recently undertook an analysis using combined *rbc*L gene and *trn*L intron sequence data from a more extensive sample of taxa (Wikström and Kenrick, 2000b). The strict consensus tree from this analysis is reproduced in figure 2 showing branch support (decay indices and bootstrap values), and subgeneric groups (sections *sensu* Øllgaard, 1987) to the right. As seen in figure 2, the analyses support monophyly of both *Lycopodium* and *Lycopodiella* as well as monophyly of the sections. Branch support is however relatively low for a number of groups and some of the questions concerning

relationships among subgeneric groups remain unresolved. There are however some interesting patterns that not only provide an opportunity to calibrate the tree against the fossil record (see below) but that are supported by morphological data.

Lycopodium casuarinoides Spring. (section Lycopodiastrum) is grouped as sister to all remaining *Lycopodium*. This basal split in *Lycopodium* is supported by at least two morphological features: the lack of spore muri (Tryon and Lugardon, 1991; Wilce, 1972) and the presence of thick, lignified and sinuate sporangium cell walls in *L. casuarinoides* (Øllgaard, 1975). Both features are reminiscent of *Huperzia* and *Phylloglossum* and are best explained as retained plesiomorphic features. Another well supported grouping is the Pseudodiphasium (*Lycopodium volubile* G. Forster)—Magellanica clade. Even though there are few similarities in habit between *L. volubile* and section Magellanica, features of spore morphology (Wilce, 1972) and the absence of basal mucilage canals in their sporophylls (Bruce, 1976b; Øllgaard, 1987) support this grouping. In *Lycopodium,* two more subgeneric group relationships are supported. Section Obscura groups with section Diphasium and section Annotina groups with section Lycopodium.

Relationships within *Lycopodiella* are more difficult to resolve. The analyses of Wikström and Kenrick (2000b) included datasets from both the plastid *rbc*L gene and the plastid *trn*L intron regions. Results from the separate analyses however differed with respect to subgeneric group relationships and the support obtained in the combined analyses was moderate. The results are also somewhat surprising, considering morphological features. Section Caroliniana for example has several features, including isovalvate sporangia (Øllgaard, 1987) and absence of leaf veinal mucilage canals (Bruce, 1976b), that are best explained as retained plesiomorphic conditions. This would suggest a basal split in *Lycopodiella* separating section Caroliniana from remaining species, but such a relationship is not supported by molecular data (Wikström and Kenrick, 2000b).

Huperzia-Phylloglossum clade.—The *Huperzia-Phylloglossum* clade is by far more species diverse than the "strobilate clade", and *Huperzia* alone includes an estimated 300–400 species. The majority of these occur either as epiphytes in low to mid altitude montane rain forests of South America, Africa and South-East Asia, or as ground dwellers in open habitats of the upper montane neotropical rain forests and high altitude alpine vegetation of the Andean mountains.

Until recently, there had been no phylogenetic treatments of the group, and most taxonomic treatments document difficulties identifying discrete morphological features indicating infrageneric relationships. Øllgaard (1987) for example considered formal taxonomic decisions to be premature and considered his *H. selago* (L.) C. Martins and Schrank group to be the only reasonably distinct infrageneric entity. He did however recognize 22 informal species groups and an additional 10 subgroups (Øllgaard, 1987). Some of these are pantropical, and their distributions imply either ancient vicariance events,

possibly linked to the rifting of Pangea, or more recent transoceanic dispersal. He also recognized several different epiphytic and terrestrial groups, but it has been unclear how these are related to each other and whether epiphytism evolved once or iteratively.

To address these questions, we recently developed a phylogenetic hypothesis of *Huperzia* based on plastid *trn*L-*trn*F intron and spacer sequences (Wikström *et al.*, 1999). The analyses included 46 *Huperzia* species, representing 18 of Øllgaard's 22 informal species groups and most of the geographical regions where *Huperzia* species are found. The resulting strict consensus tree from these analyses is reproduced in figure 3 showing branch support (decay indices and bootstrap values), species groups (sensu Øllgaard, 1987), growth habit (terrestrial/epiphytic) as well as the occurrence of neotropical and paleotropical clades. The results indicate that many of the species groups recognized by Øllgaard (1987) are either polyphyletic (e.g., *H. phlegmaria* (L.) Rothm., *H. taxifolia* (Sw.) Trevisan and *H. verticillata* (L.f.) Trevisan groups), paraphyletic (e.g., *H. saururus* (Lam.) Trevisan group) or poorly supported (e.g., *H. reflexa* (Lam.) Trevisan group). The results however strongly support the existence of other interesting patterns. Epiphytism appears to have originated once within *Huperzia* with at least two independent reversals to a terrestrial habit (*H. hippuridea* (Christ) Holub and the clade including *H. saururus, H. brevifolia* (Grev. & Hook.) Holub and *H. reflexa* groups), both in the neotropics. With two exceptions (*H. ophioglossoides* (Lam.) Rothm. and *H. funiformis* (Spring) Trevisan), all the epiphytic and secondarily terrestrial species are split into a neotropical and a paleotropical clade. Within the neotropical clade, the terrestrial species in *H. saururus, H. brevifolia* and *H. reflexa* groups constitute a large, secondarily terrestrial clade. These patterns are all well supported by the *trn*L-*trn*F data and the existence of neotropical and paleotropical clades has also been corroborated by an extended *rbc*L analysis which included both neotropical and paleotropical epiphytes (Wikström and Kenrick, 2000a).

Comparing these results with respect to morphological data is difficult. There are few morphological features that can be used to define infrageneric groups, and characteristics that have been used are endpoints in morphological continua, resulting in arbitrary decisions on character state delimitations. Notwithstanding these problems, some of the patterns obtained in the molecular analyses are unexpected. For example, neotropical and paleotropical members of the *H. phlegmaria* and of the *H. verticillata* groups show conspicuous morphological similarities but, based on the molecular analyses, these morphological similarities are the result of convergent evolution. Furthermore, as homosporous plants they have usually been considered to disperse easily, but the molecular results indicate the existence of very strong biogeographic patterns within *Huperzia.* These patterns could perhaps be related to the posession of subterranean holosaprophytic gametophytes and aspects of their establishment. Similar gametophytes are however also found within *Lycopodium,* a genus that does not show corresponding patterns (Wikström and Kenrick, 2000b). Our current knowledge on aspects of the establishment and dynamics

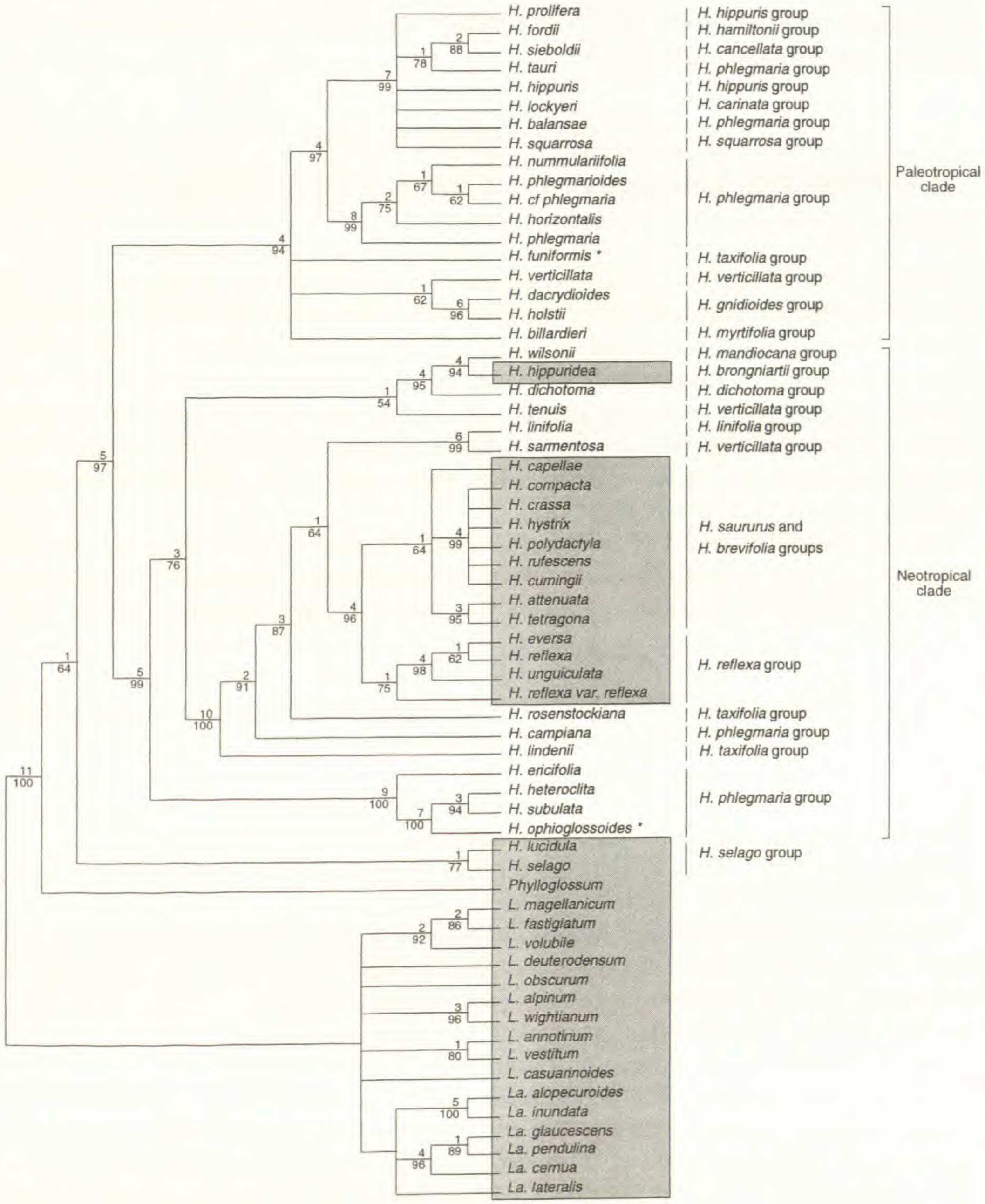

FIG. 3. Strict consensus of 16,924 most parsimonious trees indicating relationships within the *Huperzia-Phylloglossum* clade. The tree is reproduced from the analyses of Wikström *et al.* (1999) of *trn*L-*trn*F intron and spacer sequence data. Branch support is indicated by decay indices (above) and bootstrap values (below) for each branch. Informal species groups (sensu Øllgaard, 1987) are indicated to the right. The partition of epiphytic *Huperzia* into a neotropical and a paleotropical clade is also indicated. *H. funiformis* and *H. ophioglossoides* (marked with *) are exceptions to this clear biogeographic pattern. Taxa within grayed boxes are terrestrial and remaining species are epiphytic.

of lycopod populations is however limited, and before such knowledge is acquired, one can only speculate.

Patterns of Diversification

Calibration of the phylogenetic tree is critical to reconstructing the historical patterns and two approaches have been adopted. Where possible, information from the fossil record has been used. This includes the use of fragmentary plant remains, isolated organs and spores. The calibrations discussed here are however tentative and primarily based on a literature survey. As seen in figure 4, some of the calibrations based on fossil information indicate contradictory ages and further palaeobotanical work on reassembling whole plants is required. Ultimately, the fossils should of course not only be used for calibrations, but should also be included in the analyses. Attempts to correlate biogeographic data on living species with other geological data such as major tectonic events have also been done.

The macrofossil record of *Lycopodium* and *Lycopodiella* is meager (Skog and Hill, 1992). The middle Jurassic (Bajocian-Bathonian; 174 Mya) *Lycopodites falcatus* Lindley & Hutton is one of the better known species and its morphology was documented in detail by Harris (1961). He suggested an affinity with section Complanata, based on its flattened branch system with large lateral leaves and smaller dorsal and ventral leaves. If correct, this would suggest a minimum age of 174 Mya for the split between section Complanata and the clade including sections Lycopodium and Annotina (Fig. 4). Although the arguments for its lycopodiaceous affinity are convincing, critical morphological features such as stem anatomy and spore morphology are unknown and its position along the stem lineage of section Complanata as indicated in figure 4, is highly uncertain.

The mature stem anatomy of *Lycopodium* is highly distinctive with the xylem arranged in parallel bands (plectostele). This feature is characteristic of all living species. Srivastava (1946) documented what he considered to be a lycopodiaceous plectostele (*Lycoxylon indicum* Srivastava) from the Jurassic (Lias) of India (Fig. 5). Although completely decorticated, the arrangement of the xylem strands is highly reminiscent of living *Lycopodium*. This fossil evidence suggest a minimum age for the split between *Lycopodium* and *Lycopodiella* of 208 Mya (Fig. 4). The specimen of *Lycoxylon indicum* occurs in the same series of beds as *Lycopodites gracilis* Brogniart, a compression fossil that closely resembles *Lycopodites falcatus* (Skog and Hill, 1992). To determine if the two names represent different organ names for the same species would certainly contribute to our understanding of lycopod evolution.

Using fossil evidence for calibrating the tree is associated with a number of problems and potential sources of error (Doyle and Donoghue, 1993). First of all, synapomorphies shared by living taxa must be observable and recognizable in fossil taxa. Secondly, fossils only provide estimates of minimum ages and not maximum ones. If the chance of observing a particular feature is low due to a relatively meager fossil record, the minimum age implied by some rare

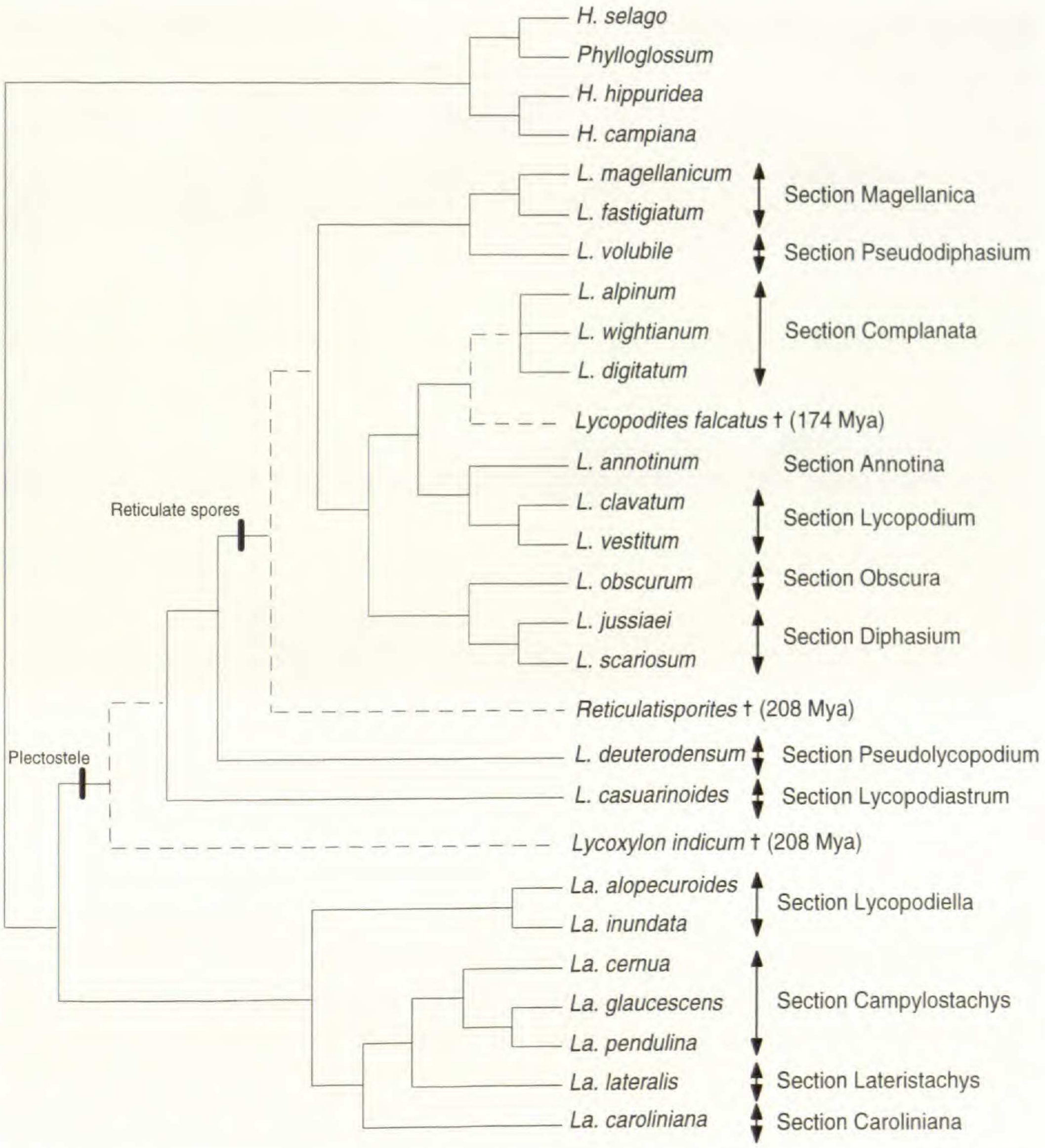

FIG. 4. Strict consensus of two most parsimonious trees from Wikström and Kenrick (2000b) including the fossils used for calibrating the tree. The fossils were not part of the analyses and have simply been inserted at the basalmost position implied by their characteristics. Ultimately the fossils should of course be included in the analyses, but our current knowledge of these fossils makes such an inclusion unfeasible at this stage.

observation of this feature can greatly underestimate the true age of its origin. Our confidence in a minimum age estimate based on fossil information therefore depends on the probability that failure of finding the feature in earlier geological records represents a "true absence" meaning it had not yet originated. In this respect, the most useful information for calibrating the ages of groups within the strobilate clade comes from the fossil spore record.

The record of fossil spores with putative *Lycopodium* affinities is quite ex-

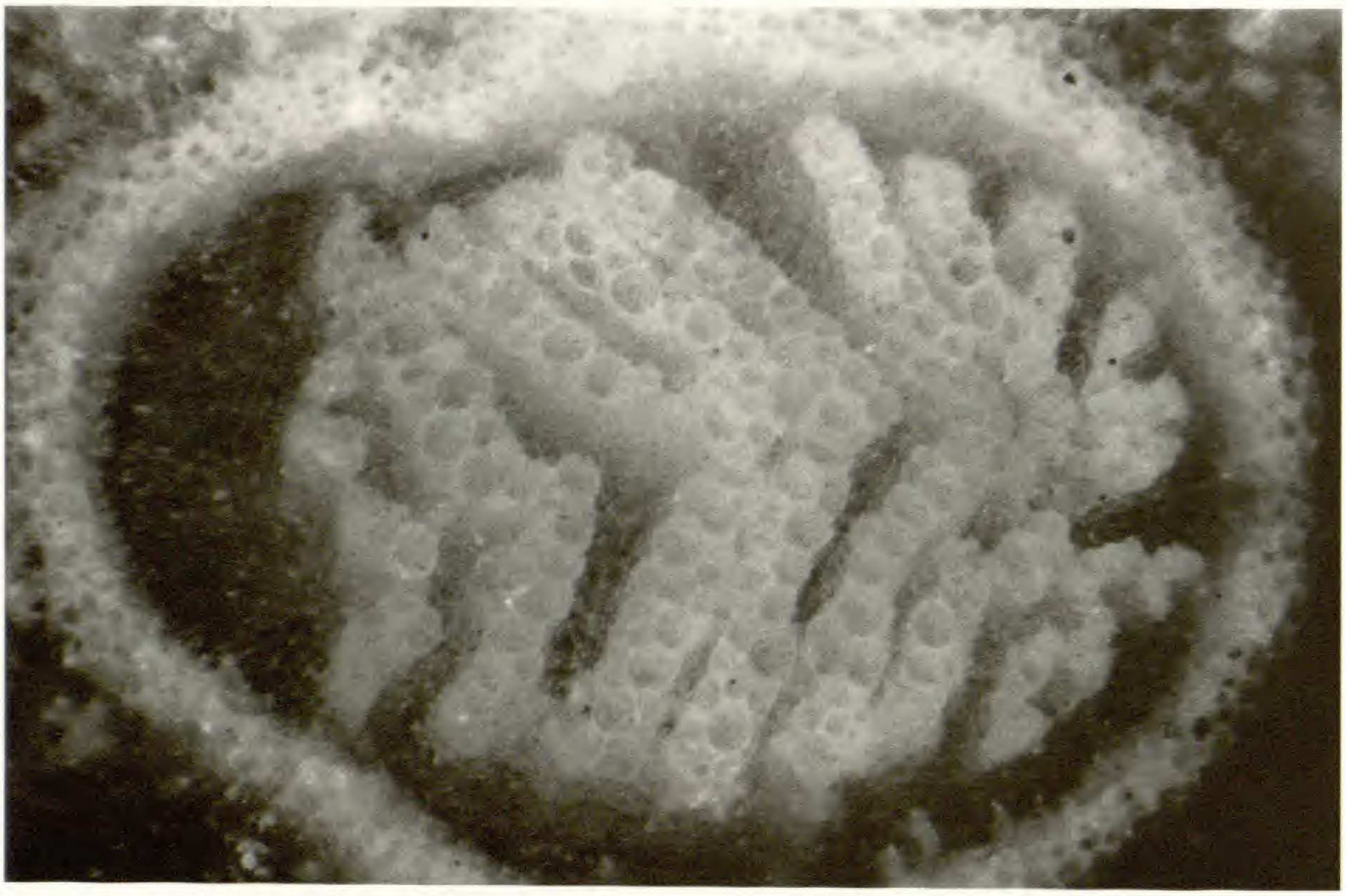

FIG. 5. *Lycoxylon indicum* (Birbal Sahni Institute of Palaeobotany, Lucknow: specimen K11/8). The fossil species was originally described by Srivastava (1946) from the Jurassic (Lias) of India. A parallel arrangement of the xylem, as seen in *Lycoxylon,* is characteristic of all living *Lycopodium* and this fossil evidence indicates a minimum age for the split between *Lycopodium* and *Lycopodiella* of 208 Mya (Fig. 4).

tensive, and there are detailed surveys of external spore morphology in living species documenting conspicuous features observable in fossil spores (Tryon and Lugardon, 1991; Wilce, 1972). Wilce (1972) recognized five different spore types within the family, four of which are found in the "strobilate clade". The rugulate type is found throughout *Lycopodiella* and the reticulate, scabrate, and bacculate types are found within *Lycopodium*. The reticulate type is typical of most species of *Lycopodium*. All but two of the living species, *L. casuarinoides* (scabrate spores) and *L. deuterodensum* Herter (bacculate spores) have this type and on the molecular phylogeny, the reticulate spore type appears as a unique synapomorphy within *Lycopodium* (Fig. 4). Fossil spores with a reticulate spore ornamentation resembling living *Lycopodium* have been documented under a number of different names such as *Retitriletes* Van der Hammen ex Pierce emend. Döring, Krutzsch, Mai & Schulz (Dettmann, 1986), *Neoraistrickia* Potonié, *Reticulatisporites* (Ibrahim) Potonié & Kremp, *Microreticulatisporites* (Knox) Potonié & Kremp, *Sestrosporites* Dettmann, *Coronatispora* Dettmann (Couper, 1953; Dettmann, 1986; Knox, 1950), *Lycopodiumsporites* Thiergart ex Delcourt & Sprumont and *Assamiasporites* Mehrotra & Sah (Kar and Mandal, 1984). Some of the *Retitriletes* species (Early Jurassic-Tertiary) are convincingly of *Lycopodium* affinity (Dettmann, 1986), and confirms the presence of *Lycopodium* by the Early Jurassic. Bharadwaj (1962) re-

ported *Lycopodiumsporites* from Upper Permian coal fields of India. Although less convincing, it indicates that early cladogenesis in *Lycopodium* may be older. Some of the reticulate fossil spores, assumed to have affinities with *Lycopodium,* will undoubtedly not survive a more critical evaluation. Others however might, and a synthesis of published data on the stratigraphic and geographic distributions of Lycopodiaceae spore fossils, and an evaluation targeted at identifying putative homologies among fossil spores and spores from living species, would clearly contribute to our understanding of the origin and diversification of *Lycopodium* and *Lycopodiella.*

About 85–90% of all living *Huperzia* species (all species groups except the *H. selago* group) are included in a tropical epiphytic clade, and the molecular results indicate that the origin of epiphytism predates a split into neotropical and paleotropical clades (Fig. 3). This biogeographic pattern is best explained by vicariance, specifically the rifting of S. America and Africa in Mid to Late Cretaceous (80–90 Mya). Biological exchange between S. America and Africa was becoming rare by this time (Taylor, 1991; Taylor, 1995; Windley, 1995) and it is therefore probable that most cladogenesis within these clades postdates the Mid Cretaceous. This conclusion is further corroborated by analyses using sequence divergence data. Results from analyses of sequence divergences using non parametric rate smoothing (Sanderson, 1997) resolve the diversification of the two clades as Late Cretaceous (Wikström & Kenrick, 2001). This implies that most modern species diversity originated in parallel with that of angiosperms (Crane, 1987). The timing and pattern of this diversification is likely related to ecological changes associated with the development of forest vegetation dominated by arborescent angiosperms.

The origin of a second monophyletic group within *Huperzia* correlates well with geological data. The clade including *H. saururus, H. brevifolia* and *H. reflexa* groups (Fig. 3) comprises an estimated 80 species and all are more or less restricted to high altitude habitats in the Andes mountains. Species of the *Huperzia reflexa* group occur in open habitats and pioneer vegetation in the transition zone between montane rain forests and the higher altitude alpine vegetation. Species of the *Huperzia saururus* and *H. brevifolia* groups include frost tolerant species and are almost exclusively found in high altitude alpine vegetation, and Øllgaard (1992) hypothesized that the *H. saururus* group originated as a response to the Andean orogeny. Results from the phylogenetic analyses confirms and extends this idea to include the *H. brevifolia* and *H. reflexa* groups. The diversification of this large, secondarily terrestrial clade seems to have been triggered by the development of open, alpine vegetation resulting from mountain building during the Andean orogeny. Mountains were probably well developed in the central Andes by the Mid Miocene (15 Mya) and in the northern Andes by the Miocene-Pliocene boundary (5 Mya; Taylor, 1995; Windley, 1995). Conservative estimates would place the origin of this secondarily terrestrial clade at about 15 Mya.

Conclusions

Available evidence indicates that most cladogenesis within the crown groups of living species of Lycopodiaceae is comparatively recent. Fossil evi-

dence provides a minimum age for basal cladogenesis in *Lycopodium* at Early Jurassic (208 Mya), and biogeographic evidence indicates that most cladogenesis within the *Huperzia-Phylloglossum* clade is even younger, postdating the Late Cretaceous (80 Mya). Considering the ancient split between homosporous and heterosporous lycopsids (Kenrick and Crane, 1997), this is somewhat surprising. The absence of family level synapomorphies however constitutes a major problem for calibrating the origin of the crown group of living Lycopodiaceae. Given our best estimate of phylogeny and our current knowledge of comparative morphology, there are no morphological features unequivocally originating along the stem lineage of extant Lycopodiaceae. Although the fossil record of Palaeozoic herbaceous lycopsids is rather fragmentary (Thomas, 1992), identifying such features would provide valuable information and could potentially provide the means for such a calibration.

The indication that the diversification of epiphytic *Huperzia* occurred in parallel with that of angiosperms, and may have been triggered and mediated by the development of angiosperm dominated rain forests may represent a more general pattern in land plants. Vitt (1984) and Buck *et al.* (2000) for example suggested a similar pattern among mosses. They hypothesized that the evolution of pleurocarpy in mosses might have been an adaptation for continuous growth and an epiphytic habit that occurred relatively recently and simultaneously with the diversification of angiosperms. This implies that perhaps as much as 70% of extant species diversity in mosses is of equally recent origin. Calibrating the origin of pleurocarpy will however be difficult considering the available fossil information. One could also speculate that similar patterns could be found within extant fern groups. The transition from a plant community dominated by pteridophytes, conifers, cycadophytes and non angiosperm seed plants to one completely dominated by angiosperms in the Late Cretaceous clearly had an enormous impact with respect to the composition and structure of the plant community (Crane, 1987). No doubt this also lead to a decrease in species diversity within a number of lineages but, at a different level, the development of a fundamentally closed canopy vegetation may also have provided new niches into which other lineages evolved and diversified.

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